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REPRODUCTIVE ECOLOGY OF DUSKY FLYCATCHERS IN MONTANE MEADOWS OF THE CENTRAL SIERRA NEVADA

James W. Cain III[1,2,3] and Michael L. Morrison[1,4]

ABSTRACT.—Avian species with expansive ranges or those that occupy more than one vegetative association may vary in aspects of their life histories across their ranges. The distribution of Dusky Flycatchers encompasses a variety of vegetative associations, including riparian communities. However, much of the literature on this species details studies conducted in upland areas. Our objectives were to describe the breeding ecology and fecundity of Dusky Flycatchers nesting in montane meadows of the central Sierra Nevada, California. We monitored 36 territories and located 37 Dusky Flycatcher nests in 8 meadows. Average clutch size was 3.9 eggs. Egg laying, incubation, and nestling stages were 4, 15.4, and 16.4 days, respectively. Eighteen nests successfully fledged young, with an average of 3.3 fledglings per successful nest. Nest success was 43% and nest predation was the leading cause of nest failure. Estimated annual fecundity was 1.62 fledglings per pair; however, because all renesting attempts were not located, this should be viewed as the minimum annual fecundity. Dusky Flycatchers we monitored may have had higher fecundity than those nesting in upland areas because riparian areas often have higher arthropod abundances. While the importance of riparian conservation to riparian-obligate bird species is obvious, our study indicates that these areas also may be of value to Dusky Flycatchers that breed in riparian areas and upland areas.

Key words: Dusky Flycatcher, Empidonax oberholseri, *reproductive ecology, nest success, life history, montane meadows, Sierra Nevada.*

Effective management of neotropical migratory songbirds requires comprehensive knowledge of life histories of individual species. Data on life histories of some species of neotropical migrants in the western U.S. are scarce (Martin 1992). Species with expansive ranges or those that occupy more than one vegetative association will likely vary in aspects of their life histories across their ranges (Sedgwick 1993a, Lowther et al. 1999). The interaction of avian life history traits and the environment is largely responsible for the fecundity of passerines (Martin 1992, Ricklefs 2000). Factors that influence avian fecundity include clutch size, nest cycle length, nesting success, and nest predation rate (Ricklefs 2000). Some factors may be influenced by environmental conditions, whereas others may not be directly influenced by the environment (Martin 1995, Ricklefs 2000).

Two major environmental factors influencing avian fecundity are nest predation and food availability (Lack 1948, Ricklefs 1969, 2000, Martin 1987, 1995), which often vary spatially within vegetation and between vegetation associations. Riparian areas produce high arthropod biomass (Jackson and Fisher 1986, Gray 1993), often have higher arthropod abundances than surrounding upland areas (Hutto 1985a, 1985b), and have fairly stable arthropod availability throughout the breeding season (Raley and Anderson 1990). However, some riparian areas also have a high number of nest predators (Ortega and Ortega 2000, Cain 2001), which may offset the potential for increased fecundity resulting from high prey availability.

The breeding range of the Dusky Flycatcher (*Empidonax oberholseri*) covers much of the mountainous area in western North America and occurs at elevations from about 650 m to 3000 m (Sedgwick 1993a). Dusky Flycatchers use a variety of vegetative associations, including the understory of mixed coniferous forests, pinyon-juniper (*Pinus-Juniperus*) woodlands, limber pine (*Pinus flexilis*)–juniper woodlands, mountain chaparral with scattered trees, aspen (*Populus tremuloides*) groves, and riparian willow (*Salix* spp.) communities (Bent 1942, Johnson 1963, Sedgwick 1987, 1993a, 1993b, Kelly 1993, Liebezeit and George 2002). Although

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Dusky Flycatcher distribution includes a variety of vegetation associations, including riparian willow communities (Morton and Pereyra 1985, Wiebe and Martin 1998, Pereyra and Morton 2001), much of the published literature on this species details studies conducted in upland areas (Johnson 1963, Sedgwick 1987, 1993b, Stahlecker et al. 1989, Kelly 1993, Liebezeit and George 2002). The importance of riparian areas during the breeding season to many riparian-obligate bird species is obvious; however, these areas may also be of value as breeding sites for species that are not riparian obligates.

Our objectives were to describe the breeding ecology of Dusky Flycatchers, including clutch size, nest cycle length, nest success and nest predation rate, and productivity in wet, montane meadows of the central Sierra Nevada, California.

STUDY AREA

Study sites are in Sierra, Nevada, and Alpine counties in the north central Sierra Nevada, California. The U.S. Forest Service manages most of the land within the study area, including the Tahoe National Forest, Lake Tahoe Basin Management Unit, and Toiyabe National Forest. The remaining land is managed by the California Department of Fish and Game or is privately owned (Bombay 1999). The study area is characterized by mountainous topography that is divided by glacial and riverine valleys. Daily summer (June–August) temperatures typically range from an average low of 4°C to an average high of 26°C. Late afternoon thundershowers are common and summer precipitation averaged 3.9 cm during our study (National Oceanic and Atmospheric Administration 1999, 2000). The study sites are wet, montane meadows surrounded by lodgepole pine (*Pinus contorta*) forests. Meadows have a north–south distribution along the east side of the Sierra Nevada crestline at elevations between 1900 m and 2700 m and range in size from 4.6 ha to 106 ha. Sedges (*Carex* spp.), grasses, and rushes (*Juncus* spp.) dominate the herbaceous plant community of the meadows, whereas the riparian shrub community is composed primarily of willows, particularly *Salix lemmonii* and *S. geyeriana* (Bombay 1999). Willow communities in the meadows often parallel streams, but they are also found scattered in clumps across the meadows. Some meadows also contain stands of mountain alder (*Alnus tenuifolia*) and quaking aspen, usually along the meadow edge. Meadows are also occupied by a variety of breeding passerines including Song Sparrow (*Melospiza melodia*), White-crowned Sparrow (*Zonotrichia leucophrys*), Willow Flycatcher (*Empidonax traillii*), Wilson's Warbler (*Wilsonia pusilla*), and Yellow Warbler (*Dendroica petechia*).

METHODS

We worked during the breeding seasons (1 June–31 August) in 1999 and 2000. When nests were found, we recorded location and number of eggs or nestlings. We monitored nests every 3 to 4 days until the nest failed or young fledged from the nest. Each time we checked a nest, we recorded number of eggs or nestlings and any evidence of nest predation or brood parasitism. Evidence of nest predation included missing eggs or missing nestlings that were ≤10 days old and were too young to have fledged. We calculated nest success using the Mayfield method (Mayfield 1961, 1975). We assumed that nest losses occurred at the midpoint between the discovery of the predation event and the date of the last nest observation.

We determined the average number of days in each stage of the nestling cycle, including only nests that were under observation for the entire stage. We assumed that the transition between stages occurred at the midpoint between nest observations. Because we did not monitor territories prior to the start of nest building, nests were found in various stages of completion; therefore, we did not attempt to determine the duration of the nest-building stage. We considered the incubation stage to be the time between laying and hatching of the 1st egg in the clutch. We considered the nestling stage to be from hatching of the 1st egg to fledging of the last nestling (Sedgwick 1993a, 1993b). We used the program CONTRAST to determine if survival rates of Dusky Flycatcher nests varied between years (Hines and Sauer 1989). The height from the ground to the bottom of all nests was measured to the nearest centimeter after the nests had either failed or fledged young.

RESULTS

We located 37 Dusky Flycatcher nests in 8 meadows. Based on the spatial distribution of territories, we are fairly confident that the nests occurred on at least 36 different territories. The earliest nest found was located during the nest-building stage on 3 June, and the last nest fledged on 26 August. Seventy-eight percent (n = 29) of nests were initiated between 1 June and 14 June, 14% (n = 5) between 15 June and 30 June, and 8% (n = 3) after 1 July (Fig. 1). All nests were located in willow shrubs in the crotch of 2 or more branches. Thirty-three nests were in *Salix lemmonii*, 4 in *S. geyeriana*. Nest height ranged from 0.05 m to 2.32 m ($\bar{x}$ = 1.18 m, $s_{\bar{x}}$ = 0.08, n = 37).

Survival rates of Dusky Flycatcher nests were not significantly different between years (χ^2 = 0.3124, df = 1, P = 0.576); therefore, we combined nest data for both years. Length of the egg-laying stage varied from 3 to 5 days, with a mean of 4 days ($s_{\bar{x}}$ = 0.07 days, n = 21 nests). The number of eggs per clutch ranged from 3 to 5 and mean clutch size was 3.9 eggs ($s_{\bar{x}}$ = 0.08 eggs, n = 28 nests) for nests located before hatching. Four nests (14.3%) had 3 eggs, 23 nests (82.1%) had 4 eggs, and 1 nest (3.6%) had 5 eggs. The incubation stage varied from 13 to 16 days with a mean of 15.4 days ($s_{\bar{x}}$ = 0.21 days, n = 15 nests). The nestling stage was highly variable and ranged from 12 to 20 days with mean of 16.4 days ($s_{\bar{x}}$ = 0.52 days, n = 15 nests).

Eighteen nests successfully fledged ≥1 young. Mean number of fledglings per successful nest was 3.33 ± 0.21 (range 1–4, n = 18 nests). Ten nests (55.6%) fledged 4 young, 5 nests (27.8%) fledged 3 young, 2 nests (11.1%) fledged 2 young, and 1 nest (5.6%) fledged 1 young. Approximately 51% (19 of 37 nests) of all nests failed; 18 of 19 (94.7 %) failures were due to nest predation. One nest (5.3%) failed due to a severe thunderstorm. Sixteen of the nests initiated between 1 June and 14 June and 2 nests initiated between 15 June and 30 June failed due to nest predation. Of 18 depredated nests, 1 was depredated during the egg-laying stage, 12 during incubation, and 5 during the nestling stage. None of the nests monitored during this study were parasitized by the Brownheaded Cowbird (*Molothrus ater*). Nest height was not significantly different between nests that fledged and those that were depredated (t = 1.696, df = 31, P = 0.218).

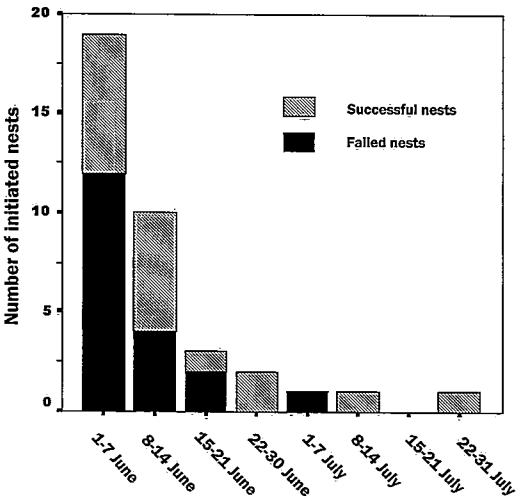

Fig. 1. Nest initiation dates for Dusky Flycatcher nests (n = 37) monitored in 8 montane meadows of the central Sierra Nevada, California, 1999–2000.

Daily survival rate for each stage in the nesting cycle was 0.990 ($s_{\bar{x}}$ = 0.010), 0.966 ($s_{\bar{x}}$ = 0.010), and 0.983 ($s_{\bar{x}}$ = 0.008) for egg-laying, incubation, and nestling stages, respectively. Based on average length of egg-laying, incubation, and nestling stages observed, the overall survival rate for each of these stages was 0.961, 0.587, and 0.755. The overall probability of a nest surviving from the beginning of the egg-laying stage until the end of the nestling stage was 0.426 (0.961 * 0.587 * 0.755).

Sixteen of the failed nests were initiated between 1 June and 14 June (Fig. 1) and likely were the 1st nest attempts for these pairs. If we assume that these pairs made a 2nd nesting attempt and had a success similar to their 1st attempt, an additional 7 nests would have been successful. If these same nests produced as many young as in the 1st nest attempts, an additional 23 fledglings would have been produced, increasing estimated annual fecundity from 1.62 to 2.24 fledglings per pair. But if the 2nd clutches were smaller and averaged 3 eggs per clutch, still approximately 18 additional fledglings would have been produced, yielding an estimated annual fecundity of 2.11 fledglings per pair.

DISCUSSION

Life history traits of Dusky Flycatchers nesting in montane meadows did not differ from

those nesting in upland environments. Nest height, mean clutch size, and mean length of egg-laying, incubation, and nestling stages we observed were consistent with those reported in other studies of Dusky Flycatchers (Johnson 1963, Pereyra 1990, Sedgwick 1993b).

Nest predation was the major cause of nest failure in our study. The predation rate we observed was lower than the 61.9% reported in a 2nd-growth ponderosa pine (*Pinus ponderosa*) forest in northern California (Liebezeit and George 2002) and comparable to the rate (53%) observed in a limber pine–juniper woodland in Wyoming (Kelly 1993). It was also comparable to the 45.6% nest predation rate calculated by Martin (1992) for shrub-nesting passerines in general.

Dusky Flycatchers nesting in montane meadows of the Sierra Nevada are exposed to a large number of potential nest predator species. Predators associated with upland forest and mountain chaparral areas, meadow/forest ecotones, and meadow interiors are active in these meadows and result in a diverse community of potential mammalian, avian, and reptilian nest predators (Cain 2001). Commonly detected predators at our study sites include short-tailed weasel (*Mustela erminea*), long-tailed weasel (*Mustela frenata*), Douglas squirrel (*Tamiasciurus douglasii*), Allen's chipmunk (*Tamias senex*), lodgepole chipmunk (*Tamias speciosus*), yellow pine chipmunk (*Tamias amoenus*), golden-mantled ground squirrel (*Citellus lateralis*), Steller's Jay (*Cyanocitta stelleri*), Common Raven (*Corvus corax*), Clark's Nutcracker (*Nucifraga columbiana*), Cooper's Hawk (*Accipiter cooperii*), Red-tailed Hawk (*Buteo jamaicensis*), and western terrestrial garter snake (*Thamnophis elegans;* Cain 2001). Although we commonly observed Brown-headed Cowbirds in our study sites, we found no brood parasitism of Dusky Flycatcher nests.

Nest success in our study was similar to that in studies conducted in upland areas (Kelly 1993, Sedgwick 1993b). The Dusky Flycatchers monitored in our riparian meadows had slightly lower estimated annual fecundity than the 1.9 fledglings per pair observed in western Montana (Sedgwick 1993b), but a higher number of fledglings per successful nest. However, because we did not account for all renesting attempts, it is likely that we underestimated annual fecundity and that the actual annual fecundity of these birds may have been similar to or higher than that reported by Sedgwick (1993b).

Nest predation and food availability have opposing influences on nest success and fecundity (Lack 1948, Ricklefs 1969, Martin 1987, 1995). The Dusky Flycatchers we monitored may have had higher fecundity than those nesting in upland areas because riparian areas often produce high arthropod biomass (Gray 1993, Jackson and Fisher 1986), have higher arthropod abundances than surrounding upland areas (Hutto 1985a, 1985b), and exhibit relatively stable arthropod availability throughout the breeding season (Raley and Anderson 1990). Furthermore, high arthropod availability has been associated with faster nestling growth rates, higher nestling weights at the time of fledging, and a higher number of nestlings fledged (Blancher and Robertson 1987, Kleindorfer et al. 1997, Turner and McCarty 1998). However, because we did not assess arthropod abundance, further research is needed to more appropriately address these issues.

Riparian areas in the western United States are limited in distribution and make up a relatively small part of the overall landscape; these areas have high species richness and densities of breeding birds and provide important habitat to many avian species (Stauffer and Best 1980, Knopf 1985, Finch 1991, Ohmart 1994). Because of the limited distribution and high species richness of riparian areas, their conservation is important for maintaining avian diversity in western landscapes (Knopf and Samson 1994). Activities such as upstream logging, poorly managed livestock grazing, and water diversions can influence hydrology, riparian vegetation, nest predation, and food availability for insectivorous birds (Kauffman and Krueger 1984, Ohmart 1994, Ammon and Stacy 1997, Rambo and Faeth 1999). While the importance of riparian conservation to riparian-obligate bird species is obvious, our study indicates that these areas may also be of value to Dusky Flycatchers and other species that are not riparian-obligates but breed in riparian areas.

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